Species competition: coexistence, exclusion and clustering

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We present properties of Lotka-Volterra equations describing ecological competition among a large number of interacting species. First we extend previous stability conditions to the case of a non-homogeneous niche space, i.e. that of a carrying capacity depending on the species trait. Second, we discuss mechanisms leading to species clustering and obtain an analytical solution for a state with a lumped species distribution for a specific instance of the system. We also discuss how realistic ecological interactions may result in different types of competition coefficients.

1. Lotka-Volterra competition and species distribution

Competitive interactions occur when entities in a system grow by consuming common finite resources. They are ubiquitous in many fields of science: examples include biological species competing for food (MacArthur & Levins 1967; Roughgarden 1979; Case 1981), mode competition in nonlinear optical systems (Benkert & Anderson 1991), or alternative technologies competing for a market (Pistorius & Utterback 1997). An early, simple, but powerful model for competitive interactions is the Lotka-Volterra (LV) set of competition equations (Volterra 1926; Lotka 1932):

$$\dot{N}_i = r_i N_i \left(1 - \frac{1}{K_i} \sum_{j=1}^{m} G_{ij} N_j \right), \quad i = 1, ..., m. \tag{1.1}$$

where m is the number of species, N_i the population of species i, r_i its maximum growth rate, K_i its carrying capacity, and G_{ij} is the matrix characterizing the interaction among species i and j, more specifically the decreasing on the growth rate of species i by the presence of j. Competitive interactions are characterized

by $G_{ij} \geq 0$, the situation to be considered here, whereas negative interactions may model situations of mutualism, predation or symbiosis.

In classical ecological niche theory, species are associated to points in an abstract *niche space*. Coordinates in this space represent relevant phenotypic characteristics, for example size of individuals in a species, or the size of preferred prey, such that intensity of competition is larger if species are closer in this space. We assume for simplicity this space to be one-dimensional (multi-dimensional generalizations are straightforward, as briefly mentioned later). If niche locations can be considered to be a continuum, we can write Eq. (1.1) as:

$$\partial_t \psi(u,t) = r(u)\psi(u,t) \left[1 - \frac{1}{K(u)} \int G(u,v)\psi(v,t)dv \right], \qquad (1.2)$$

where now $\psi(u,t)$ is the population density at niche location u. The integral extends over the full niche space, which could be finite or infinity. For most purposes, Eqs. (1.1) and (1.2) can be considered as equivalent, since the second is obtained from the first in the limit of many close interacting species, and (1.1) can be recovered from (1.2) for a discrete distribution of species:

$$\psi(u) = \sum_{i=1}^{m} N_i \delta(u - u_i), \qquad (1.3)$$

with $G_{ij} = G(u_i, u_j)$, $r_i = r(u_i)$ and $K_i = K(u_i)$.

It is widely believed that (1.1) or (1.2) predict a *competitive exclusion* leading to a *limiting similarity* situation (Abrams 1983), in which a pair of species too close in niche space can not coexist, and one of them would become extinct. However it is known that the model allows for continuous coexistence of species in some situations (Roughgarden 1979), and refinements on the conditions for this coexistence have been developed, with emphasis on the effect of the shape of the carrying capacity function $K(u)$ (Meszéna *et al.* 2006; Szabó & Meszéna 2006). In this context, a particulary surprising result was the finding by Scheffer & van Nes (2006) of a situation –for uniform carrying capacity– which was neither of full coexistence nor of full exclusion, but of clusters or lumps of tightly packed species which did not exclude each other, but were well separated from other clusters so that there was a type of limiting similarity leading to a minimum intercluster distance. Clustering of individuals or entities under competitive interactions of the LV type had been already observed in other contexts (Fuentes *et al.* 2003; Hernández-García & López 2004, 2005; Ramos *et al.* 2008), where the mechanism was the diffusive broadening of an otherwise zero-width species or entity. In contrast, the lumps in Scheffer & van Nes (2006) appeared even in the absence of diffusion in niche space, which is the situation also considered here.

The importance of the functional form of the interaction kernel G_{ij} in (1.1) or $G(u,v)$ in (1.2) was stressed by Pigolotti *et al.* (2007) for the case of uniform carrying capacity and interactions depending only on differences of niche positions, and found to be relevant in an evolutionary context by Leimar *et al.* (2008). For that case the positive-definite character of the Fourier transform of $G(u,v) = G(u-v)$ is a condition implying the absence of limiting similarity. Species clustering was reported, but for interaction functions rather different from the Gaussian used in Scheffer & van Nes (2006). In fact, for the Gaussian interaction case most results are

extremely sensitive to details such as the implementation of the boundary conditions or weak ecological second order effects (Pigolotti *et al.* 2008). Thus, a clarification of the mechanisms leading to species clustering in LV models would be desirable. In addition, the results in Pigolotti *et al.* (2007, 2008) were obtained under the unrealistic assumption of homogeneity in niche space whereas the inhomogeneities in the carrying capacity are known to play relevant roles (Szabó & Meszéna 2006). For simplicity we restrict our description to the standard situation in which competition is stronger among species closer in niche space. It is worth mentioning the existence of studies of LV systems where non-local interactions are considered (Doebeli & Dieckmann 2000). That situation can also be described by the general formalism used here of an integral kernel function, and our general results therefore also apply to the situation with non-local interactions.

In this Paper we analyse some mathematical properties of the LV model (1.1) or (1.2). In Sect. 2 we show that the positive-definiteness of the kernel G remains a determining condition for stable coexistence even for non constant $K(u)$. In Sect. 3, we discuss the mechanism producing lumped species distributions and explicitly give an analytic expression for a particular interaction kernel. In the Appendix we show that, in contrast with the earliest characterizations of the interaction kernel G (MacArthur & Levins 1967; Roughgarden 1979), both positive- and non-positive-definite kernels can arise from more detailed ecological models which consider the dynamics of the consumed resource. We use periodic boundary conditions in our numerical simulations. We expect the effects of this simplifying but unrealistic assumption to be unimportant at least when a non-constant carrying capacity limits the presence of species to a limited region of niche space.

2. The stability of close coexistence

A simplifying assumption for the study of the LV model is that of homogeneity in niche space. In this case, the carrying capacity and growth rate are constants, K_0 and r_0, and the interaction kernel depends only on differences of niche positions $G(u, v) = G(|u-v|)$. Niche space could be infinite, but in the case in which it is finite, homogeneity can only be achieved under periodic boundary conditions. Under these restrictions it is easy to see that a steady solution to (1.2) which is homogeneous and everywhere non-vanishing always exists: $\psi_0 = K_0/\hat{G}_0$, where $\hat{G}_0 \equiv \int du G(u)$. This solution represents coexistence of all possible species without a limit to their similarity. Its stability against small perturbations can be analysed by linearization of the equation resulting from substitution of $\psi(u, t) = \psi_0 + \delta\psi(u, t)$ into (1.2). The solution for the Fourier transform of the deviation from the homogeneous state, $\delta\hat{\psi}_q(t)$, is

$$\delta\hat{\psi}_q(t) = \delta\hat{\psi}_q(0)e^{\lambda_q t} \text{ , with } \lambda_q = -r_0\frac{\hat{G}_q}{\hat{G}_0} \text{ .} \tag{2.1}$$

where $\hat{G}_q$ is the Fourier transform of $G(u)$. Thus, the homogeneous solution ψ_0 is stable if $\hat{G}_q$ is positive $\forall q$, while a instability leading to pattern formation occurs when $\hat{G}_q$ may take negative values (Pigolotti *et al.* 2007; Fuentes *et al.* 2004; Hernández-García & López 2004; López & Hernández-García 2004). We note that many steady solutions to Eq. (1.2) exist besides ψ_0 (in particular, solutions of the form (1.3)). This is so because dynamics preserves $\psi(u) = 0$ at all places where

there is no initial population. Notice also that ψ_0 is the only strictly positive solution. Among this multiplicity of solutions the ones that will be more relevant are the ones which are stable under perturbations or small immigration (Pigolotti *et al.* 2007).

An interesting class of functions to be used as kernels and carrying capacities is the family $\{g_\sigma^p\}$ given by

$$g_\sigma^p(u) \equiv \exp\left(-|u/\sigma|^p\right), \qquad (2.2)$$

which is parameterized by the value of p. The widely used Gaussian kernel is obtained for $p = 2$. When $p < 2$ the functions are more peaked around $u = 0$ (the case $p = 1$ is an exponential) and for $p > 2$ they become more box-like ($g_\sigma^\infty(u)$ is the flat box with value 1 in the interval $[-\sigma, \sigma]$ and zero outside). The width of the kernel σ gives the competition range in niche space. We have positivity of the Fourier transform if $p \leq 2$. This implies that the homogeneous solution is stable under evolution with uniform K and kernel G of the form (2.2) if $p \leq 2$. When $p > 2$, the homogeneous solution is unstable and the system approaches delta comb solutions of the type (1.3), with a spacing approximately 1.4σ (Pigolotti *et al.* 2007) which represent limiting similarity situations.

We now generalize the above stability analysis to the more realistic case in which there is no homogeneity in niche space. First we consider the simpler case of a symmetric kernel $G(u, v) = G(v, u)$, which in particular includes the previous case of kernels depending only on species distance: $G(u, v) = G(|u - v|)$. Note that in this symmetric case one can write Eq. (1.2) in potential form:

$$\partial_t \psi(u, t) = -r(u) \frac{\psi(u, t)}{K(u)} \frac{\delta V[\psi]}{\delta \psi(u)}, \qquad (2.3)$$

with the functional potential given by:

$$V[\psi] = -\int K(u)\psi(u, t)du + \frac{1}{2}\int\int G(u, v)\psi(u, t)\psi(v, t)\ du\ dv. \qquad (2.4)$$

Stationary solutions of Eq. (1.2) are those for which the r.h.s of Eq. (2.3) equals 0. This has many possible solutions. We define the *natural stationary solution*, $\psi^N(u)$, as the one which is positive and non vanishing for all u, so that

$$\left(\frac{\delta V}{\delta \psi}\right)_{\psi^N} = 0, \qquad (2.5)$$

that is, the one satisfying:

$$\int G(u, v)\psi^N(v)dv = K(u)\ ,\forall\ u \qquad (2.6)$$

The solution $\psi^N(u)$ can be considered the non-homogeneous generalization of ψ_0 introduced in the homogeneous case. In the particular case in which $G(u, v) = G(u-v)$ the natural solution can be explicitly written in terms of Fourier transforms of the competition kernel and the carrying capacity, either in an infinite system or in a finite one with periodic boundary conditions:

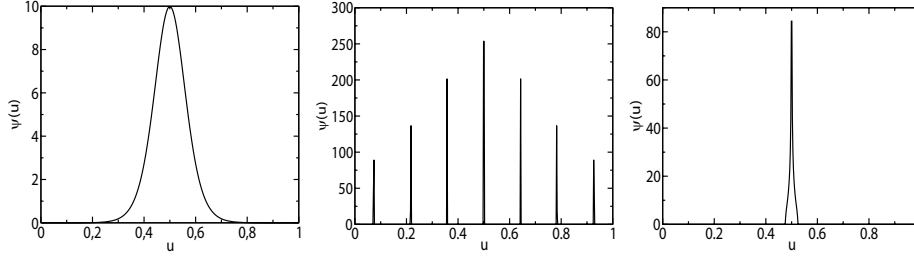$$\hat{\psi}_q^N = \frac{\hat{K}_q}{\hat{G}_q}. \qquad (2.7)$$

Figure 1. Long-time solutions of (1.2) for different kernels and carrying capacities. Left: $G = g_\sigma^1$, $K = \text{sech}(u/\sigma)$, with $\sigma = 0.1$. The natural steady solution $(\psi^N = a^{-1}\text{sech}^3(u/\sigma))$, which is positive and non-vanishing everywhere, is reached at long times. Center: $G = g_{0.1}^4$, $K = g_{0.1}^{0.5}$. Under this non-positive-definite competition kernel, the solution shown is still evolving and approaches a singular delta comb of the type (1.3) at long times. Right: $G = g_{0.1}^{0.5}$, $K = g_{0.1}^1$. A positive natural solution does not exist and the system approaches a single hump solution which vanishes in part of niche space.

This requires that these Fourier transforms and their inverses exist and lead to positive populations densities. When this happens, a continuum species coexistence is obtained, and its existence is generally robust against small changes in G or K. We show later that it is also an attractor of the dynamics when $\hat{G}_q$ satisfy positivity requirements ($p \leq 2$, for the family in (2.2), being $p = 2$ the marginal case). For a uniform carrying capacity, the natural solution (9) always exists and is uniform in phenotype space $\psi^N(u) = \psi_0$. But the natural solution may lose positivity or even cease to exist depending on the properties of G and K. For example, when both $G(u)$ and $K(u)$ are of the form (2.2) with $p = 2$, the inverse Fourier transform of (2.7) exists when the carrying capacity has a value of σ larger than the kernel G, but not in the opposite case.

Figure 1 shows stationary solutions attained at long times by the dynamics in (1.2) illustrating the situations described above, starting from a smooth non-vanishing initial condition. In the first case we choose a kernel and carrying capacity functions $(G(u) = g_\sigma^1(u)$, $K(u) = \text{sech}(u/\sigma))$ such that the natural solution exists and is positive everywhere. Thus it is stable, and it is the steady state attained at long times. In fact it can be analytically calculated:

$$\psi^N(u) = a^{-1}\text{sech}^3(u/\sigma) \ . \tag{2.8}$$

In the second case the non-positiveness of the kernel used (with a carrying capacity of the type Eq.(2.2)) breaks down the initial configuration into lumps, which at long times approach zero-width delta functions with forbidden zones in between. In the third case, despite $\hat{G}_q$ being positive, a positive natural solution does not exist. Several outcomes are possible but for the kernel and capacity used, the system approaches a single hump solution which vanishes in part of the niche space.

More in general, but still in the symmetric G case $G(u, v) = G(v, u)$, writing the LV model in potential form (Eq. (2.3)) is of great use since one can show that, provided $r(u)$ and $K(u)$ are positive, $dV/dt \leq 0$. This implies that V is a Lyapunov potential and dynamics proceeds towards its absolute minimum, or if

$\psi(u, t = 0) = 0$ for some u, towards the minimum of V under such constrain. Notice that, since the potential is a quadratic form, ψ^N is a *global* attractor (starting from non-vanishing initial conditions) when the competition kernel is a positive definite quadratic form, which means that $\int \int f(u)G(u, v)f(v)dudv \geq 0$, $\forall f$ (or $\sum_{ij} x_i G_{ij} x_j \geq 0$, $\forall \{x_i\}$ in the discrete case). This generalizes the previous stability condition on the Fourier transform $\hat{G}_q > 0$ to niche inhomogeneous cases, and shows that the stability result was global indeed. In a multi-dimensional niche space the same analysis shows that the positive-definiteness of the quadratic form remains the condition for the global stability of the natural solution. In any case, the important consequence is that the stability of the natural solution depends uniquely on the competition kernel and not on the carrying capacity (provided the relation kernel-capacity is such that the natural solution exists and is positive). In particular, for competition kernels of the form (2.2), ψ^N is always (if existing and positive) a globally stable solution of the dynamics for $p \leq 2$, and unstable otherwise.

The crucial difference in the case of a non-symmetric competition kernel is that there is no obvious Lyapunov potential for the system. This implies that there are no available global stability results. However, local stability can be investigated. Let us consider a small perturbation of the positive natural solution $\psi^N(u) + \delta\psi(u, t)$. To linear order, the perturbation evolves as:

$$\frac{d\delta\psi(u, t)}{dt} = -r(u)\frac{\psi^N(u)}{K(u)} \int G(u, v) \, \delta\psi(v, t) \, dv. \qquad (2.9)$$

We now consider the functional $H(\delta\psi) \equiv \int \, du \, \left(A(u)K(u)/r(u)\psi^N(u)\right) \, (\delta\psi)^2$, where $A(u)$ is a positive function so that $H \geq 0$ and $H(0) = 0$. Let us compute its time derivative:

$$\frac{dH}{dt} = -2 \int \delta\psi(u) \, A(u) \, G(u, v) \, \delta\psi(v) \, du \, dv. \qquad (2.10)$$

If for some choice of $A(u)$ one has that $A(u)G(u, v)$ is positive definite, then $dH/dt < 0$ and $\delta\psi = 0$ will be approached. This shows that ψ^N is linearly stable in such case. We note that the case in which $G(u, v)$ itself is positive-definite trivially guaranties the positivity of $A(u)G(u, v)$, with a constant A. Thus, even in this more general nonsymmetric case, it is the character of the interaction kernel G, and not of the carrying capacity (provided it is such that the natural solution exists and is positive), which determines the stability of the natural solution.

3. Lumped species distributions

Scheffer & van Nes (2006) found transient but long-lived solutions of Eq. (1.1) consisting of periodically spaced lumps containing many close species. They used a Gaussian interaction kernel which turned out to introduce an excessive sensitivity of the results to the numerical implementation of the model and boundary conditions (Pigolotti *et al.* 2008). They found however similar solutions as steady configurations when adding an extra predation term acting effectively only on species with high population. This can be thought as an extra *intraspecific* competition since it decreases the growth of species with many individuals. Exploiting this idea, Pigolotti *et al.* (2007) checked the effect of using in (1.2) a kernel of the type (2.2)

but with an enhanced interaction at $u = 0$, i.e. enhanced intraspecific competition. In particular, they used a constant carrying capacity $K(u) = K_0$ and a flat box kernel with an added delta function at the origin (see Fig. 2),

$$G(u) = g_\sigma^\infty(u) + a\delta(u) . \tag{3.1}$$

Lumped patterns were obtained numerically for $a = 1$.

Because the dynamics of (1.2) usually involves very long transients, it is interesting to calculate analytically the steady lumped solution in the simple case of a kernel (3.1) and uniform carrying capacity K_0 (in the infinite line).
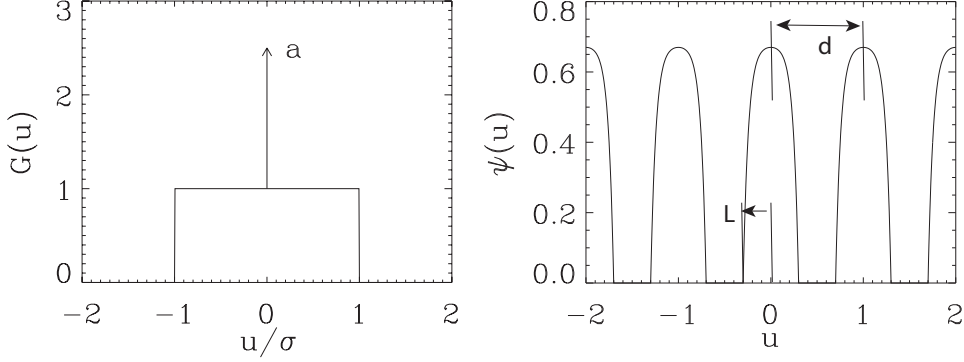

Figure 2. The kernel in Eq. (3.1) (left), and the analytic steady solution given by (3.5) and (3.8-3.9) for $a = K_0 = 1$, $\sigma = 0.8$, $L = 0.3$ and $d = 1$ (right).

We begin with the steady state condition

$$\int G(u, v)\psi(v)dv = K(u) , \tag{3.2}$$

valid at u such that $\psi(u) \neq 0$, that particularized to (3.1) and constant K reads:

$$a\psi(u) + \int_{u-\sigma}^{u+\sigma} dv\psi(v) = K_0 . \tag{3.3}$$

This is transformed into a differential-difference equation after differentiation with respect to u:

$$a\psi'(u) + \psi(u + \sigma) - \psi(u - \sigma) = 0 , \text{ where } \psi(u) \neq 0 . \tag{3.4}$$

This steady equation has many solutions, including the *natural* one $\psi_0 = K_0/(a + 2\sigma)$ which is non-vanishing everywhere, or delta combs such as (1.3). We search for solutions of the type in Fig. 2, i.e. periodic arrays of lumps, of period d, each one having a symmetric *hump* shape $f(u)$ of width $2L$ (i.e. $f(u) = 0$ if $u \notin [-L, L]$):

$$\psi(u) = \sum_{n=-\infty}^{\infty} f(x - nd) \tag{3.5}$$

We are assuming that the lumps do not overlap, so that $d > 2L$. We also note that if $\sigma + 2L < d$ there is no interaction between different lumps, so that for $u \in [-L, L]$
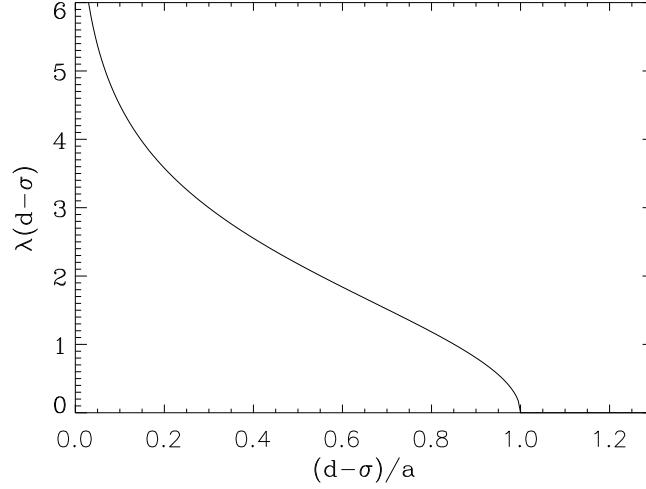
Figure 3. The solution λ (positive branch) of Eq. (3.7), giving the inverse width of species lumps. The width is finite for $d - \sigma < a$, which is favored by larger enhanced intraspecific competition a.

Eq. (3.4) reduces to $f'(u) = 0$ and there is no lump solution. Moreover, analysis is much simplified if each of the lumps interacts only with its neighbors ($\sigma + 2L < 2d$). Thus we restrict to $d < \sigma + 2L < 2d$, for which (3.4) with (3.5) and $u \in (-L, L)$ becomes:

$$af'(u) + f(u + \sigma - d) - f(u - \sigma + d) = 0 \qquad (3.6)$$

The general solution of this linear equation is obtained as a sum of exponentials $\exp(\lambda u)$, with

$$a\lambda = \sinh\left(\lambda(d - \sigma)\right) \ . \qquad (3.7)$$

$\lambda = 0$ is always a solution, and if $d - \sigma < a$ there are two additional solutions $\pm\lambda$, plotted in Fig. 3. For $d - \sigma > a$ the only solution is the constant one, but in the opposite case (the situation favored by enhanced intraspecific competition a) the solution is a linear combination of three exponentials. Two of the constants of the combination are determined from $f(L) = f(-L) = 0$. The third one, which gives the overall normalization, can be obtained by returning back to the original equation (3.3). Finally we get

$$
\begin{aligned}
f(u) &= A\left(1 - \frac{\cosh(\lambda u)}{\cosh(\lambda L)}\right) \text{ if } u \in [-L, L] \\
&= 0 \qquad \text{elsewhere}
\end{aligned}
\qquad (3.8)
$$

with

$$A = \frac{K_0}{a\left(1 - \operatorname{sech}(\lambda L)\right) + \frac{2}{\lambda}\left(\lambda L - \tanh(\lambda L)\right)} \ , \qquad (3.9)$$

and the value of λ which is plotted in Fig. 3. Figure 2 shows the analytic solution (3.5) with (3.8)-(3.9). We have not studied the stability of this configuration. But

the numerical results in Pigolotti *et al.* (2007) indicate that it is stable for some values of L and d.
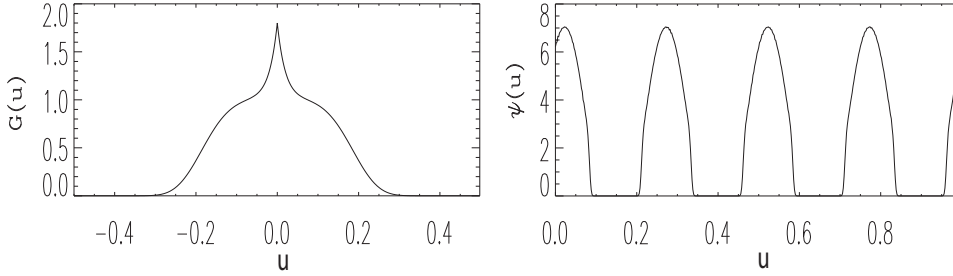

Figure 4. The kernel $G = g_{0.2}^4 + 0.8g_{0.02}^1$ (left), and the steady solution obtained numerically from it at long times with constant $K_0 = 1$ (right).

We finally stress that the appearance of the lumped solution is not a consequence of the singularity of the delta function in the kernel. In fact, any kernel sufficiently peaked at the origin will favor the coexistence of close species. If the behavior at larger distances of the kernel makes it not positive-definite, then full coexistence will be unstable and the natural solution will split into disjoint lumps. An example of the final steady state in this situation is shown in Fig. 4, with a kernel $G = g_{0.2}^4 + 0.8g_{0.02}^1$ which has the properties just described and contains no delta singularity.

Appendix A. Models leading to LV competitive interactions

We have seen that the character of the interaction kernel G is of major importance to determine the qualitative outcome of LV competition. In the original formulation of the niche model, however, only positive definite kernels were allowed. The reason is that competition kernels were derived in terms of utilization functions $u_i(x)$, describing how consumer i uses resource at niche location x (assumed to be continuous) (MacArthur & Levins 1967; Roughgarden 1979):

$$G_{ij} = \frac{\int u_i(x)u_j(x)\,dx}{\int u_i^2(x)\,dx}. \tag{A 1}$$

When the resource is directly related to space, (A 1) can be justified by considering the probability that consumer i meets consumer j (Roughgarden 1979). It is easy to see that G_{ij} obtained from (A 1) is positive definite. We show in the following, however, that relation (A 1) is by no means general, and that a greater variety of kernels –positive or non-positive definite, so that the natural solution representing coexistence can be either stable or unstable– could be obtained from equations in which resources are explicitly modelled. Related calculations could be found, for example, in Schoener (1974).

We consider a set of predators (or consumers), with populations N_i, $i = 1, 2, ...m$, competing for different types of prey populations or resources, R_α, $\alpha = 1, 2, ...n$,

the later growing in a logistic way with growth rate β_α and carrying capacity Q_α in the absence of predators. Particular equations modelling this are

$$\dot{R}_\alpha \;=\; -R_\alpha \sum_i a_{\alpha i} N_i + \beta_\alpha R_\alpha \left(1 - \frac{R_\alpha}{Q_\alpha}\right) \tag{A\,2}$$

$$\dot{N}_i \;=\; N_i \sum_\alpha S_{i\alpha} R_\alpha - d_i N_i \tag{A\,3}$$

d_i is the death rate of species i. The interaction coefficients are $a_{\alpha i}$, the depletion rate of resource α produced by species i, and the *sensitivity* $S_{i\alpha}$, giving the growth rate of i thanks to resource α. Lotka-Volterra type dynamics arises when the time scale for resource evolution is much faster than that of the consumers (i.e. $S_{i\alpha}$ and $d_i \to \infty$, but with their ratio finite). In this case, adiabatic elimination of the resource can be done ($\dot{R}_\alpha \approx 0$, so that each prey is at each instant at the equilibrium determined by their consumers), giving

$$R_\alpha \approx Q_\alpha \left(1 - \frac{1}{\beta_\alpha} \sum_i a_{\alpha i} N_i\right) \;. \tag{A\,4}$$

for the non-vanishing resources. The *impact* matrix, $D_{\alpha i}$, describing the depletion of resource α by species i (Meszéna *et al.* 2006), is $D_{\alpha i} = Q_\alpha a_{\alpha i}/\beta_\alpha$, which substituted into the consumers equation leads to:

$$\dot{N}_i = N_i \left(r_i - \sum_j C_{ij} N_j\right) \;, \tag{A\,5}$$

where $r_i = \sum_\alpha S_{i\alpha} Q_\alpha$ is the maximum growth rate and $C_{ij} = \sum_\alpha S_{i\alpha} D_{\alpha j}$. Thus, the result is an effective interaction among the predators which is of Lotka-Volterra type. It is customary to write (A\,5) in terms of the carrying capacity K_i, defined as the equilibrium population N_i attained in the absence of the other competitors, i.e. $K_i = r_i/C_{ii}$. In terms of it, Eq. (A\,5) becomes identical to (1.1), with

$$G_{ij} = \frac{C_{ij}}{C_{ii}} = \frac{\sum_\alpha S_{i\alpha} D_{\alpha j}}{\sum_\alpha S_{i\alpha} D_{\alpha i}}. \tag{A\,6}$$

Having a continuum $R(x)$ of resources instead of a discrete set R_α does not introduce important difficulties. Simply one should replace sums by integrals, replacing the coefficients of Eq. (A\,5) by:

$$r_i \;=\; \int S_i(x) Q(x) dx \;, \tag{A\,7}$$

$$C_{ij} \;=\; \int S_i(x) D_j(x) dx \;, \tag{A\,8}$$

$$G_{ij} \;=\; \frac{\int S_i(x) D_j(x) dx}{\int S_i(x) D_i(x) dx} \;, \tag{A\,9}$$

One can also consider a continuum of species, labelled by their phenotypes u, so that Eq. (1.1) is replaced by Eq. (1.2) with $K(u) = r(u)/C(u,u)$, $G(u,v) =$

$C(u, v)/C(u, u)$, and $r(u)$ and $C(u, v)$ given by obvious generalizations of (A 7) and (A 8).

It is clear that the presence in the kernel G_{ij} of two different functions (compare with the most restrictive expression (A 1)) gives enough freedom to obtain a variety of kernel behaviors under different circumstances. A particularly popular choice is to assume that impact and sensitivity are proportional: $S_{i\alpha} = \epsilon D_{\alpha i}$, with a constant efficiency ϵ. In the continuum resource case the functions can be written in terms of a single utilization function $u_i(x)$ as $D_i(x) = u_i(x)$ and $S_i(x) = \epsilon u_i(x)$, leading to the classical expression (A 1). Slightly more general cases arise when the efficiency depends only on the resource, $\epsilon = \epsilon_\alpha$, or on the consumer $\epsilon = \epsilon_i$, or when dependence on the two types of species factorizes, $\epsilon = v_i w_\alpha$. In all these cases (if the efficiency is positive) one is lead to a kernel G_{ij} which is positive definite. In more general cases, one can have a kernel leading to instability of the coexistence state.

We conclude with two instances of ecological interactions in (A 3) which allow to tune the stability. First, a homogeneous discrete and infinite niche space in which all resources have the same internal dynamics $Q_\alpha = Q$, $\beta_\alpha = \beta$, $\forall \alpha$, as well as the consumers: $d_i = d$, $\forall i$. The interactions are taken to be

$$S_{i\alpha} = g\delta_{i,\alpha} \tag{A 10}$$

$$a_{\alpha,j} = \frac{\beta}{Q} D_{\alpha j} = a\delta_{\alpha,j} + b(\delta_{\alpha,j-1} + \delta_{\alpha,j+1}).$$

This models a situation in which the consumer k grows only by consuming its optimal resource R_k, whereas it depletes also the neighboring resources, R_{k+1} and R_{k-1}. We have $r_i = Qg$, $K_i = \beta/a$, $C_{ij} = (Qg/\beta)(a\delta_{i,j} + b(\delta_{i,j-1} + \delta_{i,j+1}))$, and $G_{ij} = \delta_{ij} + (b/a)(\delta_{i,j-1} + \delta_{i,j+1})$ so that equation (1.1) is now

$$\dot{N}_i = QgN_i \left[1 - \frac{1}{\beta} (aN_i + b(N_{i+1} + N_{i-1})) \right]. \tag{A 11}$$

The natural solution, i.e. the one in which all species have positive non zero population, is $\overline{N}_i = \beta/(a + 2b)$, $\forall i$. Its linear stability can be studied by linearization, $N_l(t) = \overline{N}_l + \delta N_l(t)$ and substitution of the ansatz $\delta N_l \approx e^{\lambda_q t} e^{iql}$ (here $i = \sqrt{-1}$). We find $\lambda_q = -(Qg/\beta)(a + 2b\cos q)$, $q \in [-\pi, \pi]$. λ_q are the eigenvalues of $-C_{ij}$, and stability of $\overline{N}_i$ requires all these eigenvalues to be negative, i.e., C_{ij} to be positive definite. When $a > 2b$, then $\lambda_q < 0$ $\forall q$, and the natural coexistence solution is globally stable (see results in Sect. 2). It is unstable otherwise. In this example, there is no well-defined single utilization function and the positivity properties of the interaction kernel and thus the stability of the natural solution can be changed by varying the parameters.

As a second example, with nonconstant carrying capacity, we consider a continuous distribution of resources and species on the line, and we take

$$\begin{aligned} Q(x) &= Qg(x), & \beta(x) &= \beta g(x), \\ S_u(x) &= s\delta(u - x), & a_u(x) &= f(u - x). \end{aligned}$$

which implies that the consumers of phenotype u grow only from the resource at location $x = u$, but they deplete a wider range characterized by f. This leads (in the continuous formalism) to $r(u) = sQg(u)$, $C(u, v) = sQf(u - v)/\beta$, $K(u) =$

$\beta g(u)/f(0)$ and $G(u,v) = f(u-v)/f(0)$. In this example, by choosing the functions g and f, we can impose any desired combinations of carrying capacity and interaction kernel. Gaussianity or positive definiteness are particular cases, no more natural in this generalization than alternative choices leading to non-positiveness, instability, and thus exclusion zones between clumps of species.

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